Towards standardized descriptions of the echolocation calls of microchiropteran bats: pulse design terminology for seventeen species from Queensland

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ABSTRACT

The identification of Australian microchiropteran bats using acoustics is in its infancy, with the Anabat System (Corben 1989) predominantly being adopted as a tool to undertake such a task. Although species-significant call characteristics of free-flying bats have not been documented, identification of bats is generally achieved by comparison of recorded calls with calls accompanying the software and/or release calls of captured bats. This practice can be unreliable if a mechanism to describe the call characteristics is not in place for workers to describe their assessments. A much needed part of this mechanism is a common language of ultrasonic terms to facilitate the exchange of information among bat workers. By way of contributing to this need, a terminology to classify the structure of calls (shapes) and another of call parameters was developed. A selection of call parameters, based on international microchiropteran literature, was adapted for Anabat use. The proposed terminologies were used, with the measurement of chosen parameters of selected recordings, to describe some of the call characteristics of seventeen species of microchiropteran bats occurring in southeastern Queensland.

INTRODUCTION

The study of microchiropteran bats in Australia is proceeding with some difficulties, such as in aspects of sampling methods, taxonomy, species identification from echolocation calls, data analysis and terminology. The topics addressed in this paper are derived from experience with the Anabat System (Corben 1989), an ultrasonic instrument to identify microchiropteran bats from their echolocation calls. These topics relate to species-significant call characteristics, with the aim of producing a practical outcome to describe such characteristics.

Microchiropteran bats hunt and perceive their surroundings by emitting short pulses of high frequency sounds and interpreting the returning echoes. This perception was termed echolocation by Griffin (1944). A bat call, or call sequence, consists of several pulses or train of pulses separated by pauses controlled by the bats. Different bat species emit different calls, reflecting their morphology and habitat use. Furthermore, intraspecific variations in the structure of calls, termed pulse design, is common. Such differences have been attributed to behaviour (Obrist 1995; Thomas et al. 1987), age (Jones and Kokurewicz 1994), sex (Jones and Ransome 1993) or varying hunting strategies used in different foraging habitats (Schumm et al. 1991). Brigham et al. (1989), postulated that variation in pulse structure may result

from genetic differences between individuals within a population, or that they may have a communicative function, or result from morphological differences in vocal structures.

The structure of calls, or the pulse design (shapes), differs according to the analysis applied to interpret bat signals. However, each bat species is likely to use several shapes to gain information on habitat and prey distance and size. Aldridge and Rautenbach (1987) found a correlation between the shapes and wing morphology and habitat use. These variations complicate the acoustic identification of bats, or any attempt at describing the full spectrum of calls each species utilizes in different situations.

A common terminology addressing features of echolocation calls is non-existent, apart from basic terms used such as CF (Constant Frequency), FM (Frequency Modulated), Search or Attack Phases and Feeding Buzz (Griffin 1958).

Simmons and Stein (1980) expanded a system proposed by Simmons et al. (1975) to classify sonar signals into identifiable categories. Simmons' and Stein's system used the presence and arrangement of CF and FM elements in the waveform of sonar signals, including consideration of the harmonic and amplitude features of the call. This system is inappropriate for the classification of call sequences generated by Anabat detectors,

whose output records the dominant harmonic of the call pulses but not the amplitude modulation and harmonic content (Corben 1989). This is not a problem for the Anabat detectors, which have been designed as an inexpensive, robust and simple microchiropteran inventory and identification tool (Corben 1989).

This paper presents a system to classify the different pulse shapes based on signals interpreted from the Anabat II System. Further, by applying this system with the measurement of selected parameters of microchiropteran echolocation calls recorded in south-east Queensland, it describes some of the features of the most common pulse shapes of seventeen species.

MATERIALS AND METHODS

Ultrasonic signals of free-flying bats were recorded using the Anabat II bat detector system (Titley Electronics, Ballina, New South Wales) (Corben 1989), throughout South-east Queensland. Signals were recorded either on cassette tapes using Realistic VSC-2001 tape recorders, or into a Toshiba T100SE portable computer by connecting the detector to an interface module (ZCAIM, Titley Electronics, Ballina, New South Wales) immediately after being emitted by bats. Signals recorded onto tapes were later processed through the ZCAIM, which employs zero-crossing analysis refined from the original concept of Miller and Degn (1981) and feeds dedicated IBM software Anabat 5 version 2.b with the necessary figures to plot frequency/time graphs used for subsequent species identification. The parameters used for species identifications were based on information generated by Anabat. These were frequency, pulse duration, pulse interval and shape.

Identified sequences were grouped by their quality (high signal to noise ratio, longer than one second duration, no more than one bat recorded per sequence, search phase sequences) and a subset was selected for measurement. The selection was based on the type of pulse shapes. Only sequences containing mainly the most common pulse shape emitted by each species were chosen. Sequences were inspected on magnification F7 in Anabat, except otherwise indicated. This magnification produces an x-axis with a total width of 150 milliseconds. Average and Standard Deviation of the measurements were calculated (Table 1).

Frequency and temporal patterns of the selected sequences were measured by using the frequency (KHz) and time (ms) cursors provided. A maximum of six pulses was

measured in each sequence, but in some cases only one pulse was measured (Table I). Another exception was the Little Pied Bat Chalinolobus picatus, due to few available sequences. Twenty-one pulses were measured from a single sequence obtained prior to the collection of a free-flying bat, recorded with the portable computer.

PULSE TERMINOLOGY OF ULTRASONIC CALLS

I consider that five basic pulse shapes characterize the calls from bats of south-east Queensland (Fig. 1). These are classified as basic shapes and are the foundation and building blocks for other call shapes. This foundation is modified by alteration in the frequency pattern of pulses, a total of seven frequency features were identified and bring forth another group of characteristic shapes, termed variant shapes. The variation results in eleven variant shapes being identified. The shapes employed by each species are not always used in the same sequence.

I have given the basic shapes a code in upper case (F, FM-CF-FM, L, R and C, Fig. 1), whereas the frequency features appear in lower case (i, s, x, d, o, b and t, Fig. 1). A variant shape may have more than one feature and, in this case, it will have a three letter code (e.g., dsR, dtC, obC).

These abbreviations state the following:

F = Flat, FM-CF-FM = Constant Frequency, L = Linear, R = Right-angled, and C = Curvilinear; i = inclined, s = short, x =extended, d = decreasing, o = open, b = bi (two), and t = tri (three).

The terminology of the shapes is based on the frequency features of the different pulses. The definition of each term is given below and is best read in conjunction with Figure 1:

- "Flat" refers to a pulse of constant frequency applied to members of the Molossidae and Emballonuridae families.
- "Constant Frequency" pulses are composed mainly of one constant frequency component but also possess frequency modulated components. The pulse design described here was adapted from Simmons and Stein (1980) to avoid divergence from widely used description of rhinolophids and hipposiderids pulses and it is only applied to the Eastern Horseshoe-bat Rhinolophus megaphyllus. In this case it consists of a long constant frequency component in the middle of two short frequency modulated components. The first

Table 1. Measurement of selected parameters of echolocation calls of seventeen microchiropteran bat species recorded in south-east Queensland.

RAT SPECIES	ALTERNATING N PULSES SHAFE	N PULSES	SHAFE		FREQUENCY B	ENCY BANDWIDTH		CHARACT	CHARACTERISTIC FREQ.	REQ.	FINAL	FINAL PREQUENCY	5	DURA	DURATION		PULSE INTERVAL	EKAYT	
selected calls (N)	pulses	measured	type	highest range	lowest	mean band	max band	гапде	теап	s. dev.	range (N)	mean	s. dev.	гапде	mean	s. dev.	range (N)	mean	s, dev.
Mornopterus norfolkensis (8)	Lower pulses Higher pulses	23 13	dF dF	N/A N/A	N/A N/A	32.5 34.4	33.5–31 35.5–33.5	33.5-31 35.5-33.5	32.3 34.4	0,76	31.5-29.5 34.5-30	30.5 32.4	0.66	10.5-5.5	7.2 6.25	1.35 0.62	160-76.7 (19) 138-85 (12)	109.7 114.6	16.3 15.8
Mormopterus beccarii (12)	N/A	62	SWF	29.5-20.5	23.5-19.5	23.4-21.6	29.5–19.5	23.5–19.5	21.6	0.95	N/A	N/A	N/A	20-11.5	14.9	2.12	424-209 (46)	318.6	56.5
Saccolaimus flaviventris (13)	N/A	50	SwF	31–23.5	25-19.5	26.6-21.4	31-19.5	25-19.5	21.4	1.85	24-18.5	20.6	1.88	14.5-6.75	10.2	1.62	475–188	288	08
Tadarida australis (6)	N/A	61	SwF	15.5-13	12-10.5	13.8-11.1	15.5-10.5	12-10.5	11.1	0.31	N/A	N/A	N/A	21.8-13	16.9	2.32	1021–700	829	150.75
Myotis moluccarum (10)	N/A	55	L	72-57.5	39-35	76.4–36.9	72-35	N/A	N/A	N/A	N/A	N/A	N/A	9.25-3.75	6.2	1.36	99.5–57.8 (42)	73	11.66
Miniopterus australis (11)	N/A	38	R	72.5-61.5	59.5-56.5	66.5-58.5	72.5–56.5	59.5-56.5	58.5	0.71	58-53	56.3	2.02	9-5.5	6.45	0.0	99.3–50 (36)	71.1	10.9
Miniopterus schreibersii (24)	N/A	53	R	58.5-48	46-42.5	51.4-44	58.5-42.5	46-42.5	44	98.0	N/A	N/A	N/A	10.3-6.25	8.2	1.04	131-62.5 (38)	96	14.3
Vespadelus pumilus (28)	Lower pulses Higher pulses	70	õõ	89-68 78-60	56-50.5	74–53.4 68.9–54.3	99–50.5 78–52	56-50.5 56-52	53.4 54.3	1.22 1.4	58–52 57–53	55 55.5	1.22	6-3.25	4.3	0.61	90.8-61.4 (66) 93.8-73.9 (5)	79.5 86.1	7.75
Vespadelus troughtoru (11)	N/A	57	s.R	60.5-51.5	51-48	54.5-49.1	60.5-48	51-48	49.1	0.7	N/A	Y/A	¥ _N	7.25-4.5	5.96	0.61	94.2-75.1 (21)	85.3	98'9
Chalinolohus gouldii (36)	Lower pulses Higher pulses	71 44	24.24	52-34 52.5-36.5	30.5-27 33.5-28	40.6–28.4 44.5–30.6	52-27 52.5-28	30.5-27 33.5-28	28.4 30.6	0.92	N/A N/A	N/A N/A	N/A N/A	9.25-4.75 9.25-4.75	7.6.5	0.93	130-80.5 129.5-88.5	112.5 110.9	10.9
Chalinolobus morio (21)	Lower pulses Higher pulses	54 26	Ω̈́Ω	77.5–55.5 77.5–58.5	54.5-50 55-51.5	67.4-52.3 67.1-53	77.5–50 77.5–51.5	54.5–50 55–51.5	52.3 53	1 0.96	56.5-50 56.5-53	53.9	1.04 24.0	6-3.25 5.5-3.75	4.8	0.64	94.9–52.4 (45) 95.5–60 (21)	77.5 80.4	11.3 8.6
Chalinolobus nigrogriseus (23)	Lower pulses Higher pulses	87 6	s.R s.R	50-40.5 47.5-42.5	39.5-36.5 40-38.5	44.6-38.1 44.6-39	50-36.5 47.5-38.5	39,5-36.5 40-38.5	38.1 39	77.0 0.63	N/A N/A	N/A N/A	N/A N/A	9.75-4.75 6.5-5.25	6.4 5.8	0.83	128-84.8 (58) 104-91.3	106.3	10 5.32
Chalinolobus picatus (6)	Lower pulses Higher pulses	31 9	sR sR	51.5-43 51.5-45.5	44.5-40	46.4-41.4 49.2-43.6	51.5-40 51.5-43	44.5-40 44.5-43	41.4	1.15 0.5	N/A N/A	N/N N/A	N/A N/A	9.25-3.5 6.5-5.25	5.6	1.4	103-75,1 (20) 104-91.3	88.8 83.1	9.7 6.03
Scotorepens greyii (20)	N/A	99	βÇ	60-44	40.5-37.5	50.5-39.1	60 -37.5	40.5-37.5	39.1	8.0	42–38.5	40	96.0	7-4.5	5.7	0.62	115-90.5 (65)	103	6.74
Scotorepens orion (5)	N/A	19	35	67-51	36.5-32	57.3-34.8	67-32	36.5-32	34.8	1.37	N/A	N/A	N/A	12.3-8	10.5	1.3	138-112 (14)	129.2	6.71
Scoteanax rueppellii (7)	N/A	23	Ş€	61-42.5	36.5-31.5	50.2-33.6	61-31.5	36.5-31.5	33.6	1.03	N/A	N/A	N/A	14.8 -9.5	12	1.47	143–102 (15)	127	12.7
BAT SPECIES	SHAPE		E	FM 1 (N = 81 pulses)	**	D C	F (N = 81 paises)			N.	FM 2 (a = 81 pulses)	1		Ц	DURATION	N	PULSE	PULSE INTERVAL	
selected calls (N)	type	highest range	lowest range	mean band	max band s. dev.	highest	mean lowest CF	s. dev.	highest range	lowest range	mean band	max band	s. dev.	range	mean	n s. dev.	range (N)	mean	s.dev.
Rhinolophus megaphyllus (20) FM-CF-FM	(0) FM-CF-FM	68-65	64.5–58	61.1-66.7	64.5-65 20.6-0	69 0-	65.5 67.8	0.88	68-65 66	66.5–54.5	66.7-61.5	68-54.5	0.78-3.2	2 73.5-41.5	5 53	7.4	117-71.6 (78)	87.9	10.5

FM component briefly increases in frequency, whereas the second briefly decreases in frequency.

- "Linear" reflects a very steeply sloped pulse decreasing rapidly in frequency over time.
- "Right-angled" is a pulse changing in frequency on a right angle slope.
- "Curvilinear" pulses feature a more gentle angle of slope than Linear pulses.
- "Inclined" refers to a flat pulse that retains its constant frequency characteristic only at the end, thus featuring a gentle sloping start.
- "Short" refers to pulses with a much lower start frequency than typical Right-angled pulses.
- "Extended" refers to Linear pulses that possess a 'tail' (or a very brief Characteristic Frequency, see Other Proposed Terms). Such variants resemble bi-Curvilinear pulses and are identified by the rapid change in frequency at the start of the pulse, ranging from at least 20 to 30 KHz in a few milliseconds (3-5).
- "Decreasing" refers to those pulses which decrease in frequency close to their termination.
- "Open", refers to the wide-angled nature of certain bi-Curvilinear pulses.

- "Bi" refers to Curvilinear or Linear pulses with two distinct curves.
- "Tri" refers to Curvilinear pulses with three curves, where the last curve increases in frequency.

FREQUENCY TERMINOLOGY OF ULTRASONIC CALLS

Frequency was analysed in four ways: Frequency Bandwidth; Characteristic Frequency; Final Frequency and Alternating Pulses.

- 1. The Frequency Bandwidth was determined by matching the frequency cursor at the start and the end of each pulse, the limits of each were termed Highest range and Lowest range (Fig. 2).
- 2. Characteristic Frequency is the frequency with the longest duration in each pulse, i.e., where the signal spends most time at (the flattest part of the pulse). It equates to the highest frequency in bats emitting Constant Frequency (CF) signals and the lowest to Frequency Modulated (FM) bats. Bats emitting steep modulated signals (Linear, L) only present a Characteristic Frequency when emitting their variant shape (extended Linear i.e., xL, Fig. 1).
- 3. Most pulses end at the Characteristic Frequency. When this is not the case a Final Frequency is displayed (Fig. 2). This can be higher or lower than the Characteristic Frequency, for example,

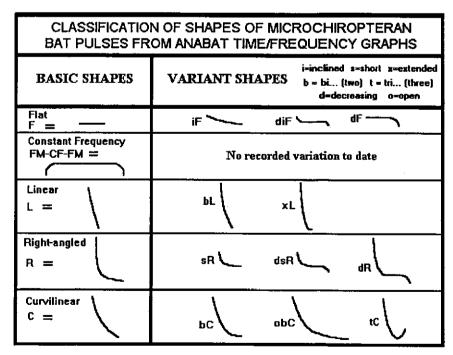


Figure 1. A classification of pulse shapes from ultrasonic calls, recorded by the Anabat II System.

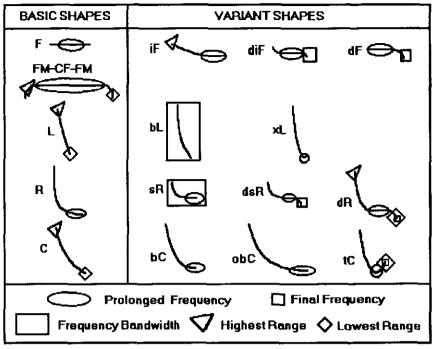


Figure 2. Frequency parameters chosen for measurement (see Table 1).

higher in the case of tC pulses and lower in dR, dF, dswF, and dsR pulses.

4. Alternating Pulses (lower and higher pulses, Fig. 3 and Table I). Frequency/time graphs are artificial displays of bat calls, which vary according to the analysis applied to their signals. Zero-crossing analysis provides data only on the frequency and temporal patterns of recorded calls. No envelope or harmonic structure is retained and Anabat responds to the dominant harmonic present in

any signal. However, some species (e.g., Chalinolobus gouldii, Vespadelus pumilus, Table 1) quite commonly emit pulses on slightly different alternating frequencies, producing consecutive higher and lower frequency pulses. This feature can be highly diagnostic of particular species, and as such it was measured for the species in which it occurred. Measurements applied to the alternating pulses were the same as those applied to all other pulses.

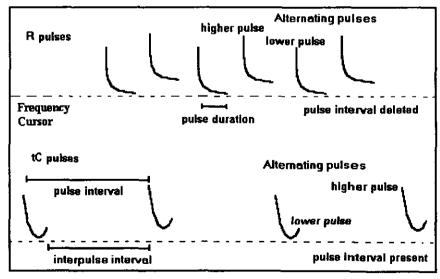


Figure 3. Temporal patterns and pulse alternation.

The temporal patterns measured were duration of pulses and pulse interval:

- "Pulse duration" (the length of the pulse).
 It was manually measured using the time cursor.
- 2. "Pulse interval" (the period between the start of two pulses). It is automatically given by Anabat. Some pulse intervals were rejected because of natural pauses occurring between selected pulses and could lead to their over quantification. This resulted in a smaller number of pulses being measured for this parameter. This number is stated after Pulse Interval Range on Table 1. In order to avoid the natural pauses going unnoticed while measuring, smaller magnifications F6, F5 and F2 instead of F7, were used to measure pulse interval. These magnifications produce an x-axis of 275, 759 and 7 500 ms respectively.

RESULTS

A compilation of the results obtained is presented in Table 1, including average and standard deviation of measurements. Utilizing this system to classify the pulse shapes leads to the contrast, according to the type of basic shape pulses employed by its members, among families of microchiropteran bats of south-east Queensland. One member of the Rhinolophidae family, Rhinolophus megaphyllus, emits only FM-CF-FM basic pulses, no variant shapes were recorded. Emballonurids and molossids employ F pulses. Vespertilionids employ L, R or C pulses. Assigning the appropriate variant

shapes to the species leads to further grouping (Table 2).

Different species calling at the same frequency range pose a strong challenge to their identification. Furthermore, if these species emit the same pulse shape, identification may not be possible using the Anabat system. Fortunately, quantification of some parameters may be of some assistance. The Yellow-bellied Sheathtail-bat Saccolaimus flaviventris, and Beccarii's Freetail Bat Mormopterus beccarii, emit signals at around 20 KHz, and commonly swF pulses. One difference separating these two species is that M. beccarri usually emits longer pulses. Two similar species, the Little Pied Bat Chalinolobus picatus, and the Hoary Bat Chalinolobus nigrogriseus, are distinguished by the former emitting pulses at a higher frequency shown by the range and mean of the prolonged frequencies.

Some species are difficult to differentiate, there being only subtle differences in the average of the measurements. The Greater Broad-nosed Bat Scoteanax rueppelli and the Eastern Broad-nosed bat Scotorepens orion are difficult to identify acoustically. Selected sequences were identified based on visual cues of individual's relative size and flight behaviour at time of recordings (Chris Corben, pers. comm.). This technique is also used by European workers (Ahlen 1992). Note that the shape of the pulses in these two species can be readily distinguished from other Scotorepens species due to the much wider angle (Table 2). A larger data set and different approach could identify more reliable differences between these two species.

Table 2. South-east Queensland Microchiropteran bats grouped according to the type of pulse shape.

Basic shape	Variant shapes	South-east Queensland species
CF	N/A	Rhinolophus megaphyllus
F	iF, diF	Saccolaimus flaviventris, Mormopterus becarii, Nyctinomus australis
	dF	Mormopterus norfolkensis
L	bL	Myotis spp.
	хL	Nyctophillus spp.
R	sR, dsR, dR	Miniopterus australis, M. schreibersii, Chalinolobus gouldii, C. nigrogriseus
	sR	Chalinolobus picatus
	sR, stC and tC on attack	Vespadelus throughtoni
	obC	Scotorepens orion, Scoteanax rueppellii
С	bC, tC	Scotorepens greyii
	tC, bC	Vespadelus pumilus, C. morio

DISCUSSION

The absolute identification of bat species using acoustics should be possible where a full spectrum of calls, given by all species within a geographic region, have been documented. In south-eastern Queensland, not all the calls have been documented. The absence of call recordings is due to either the rarity of some species (e.g., Chalinolobus dwyeri) or lack of opportunity.

The measurements presented here provide a representation of the most common call of each species. It is not intended to be a definitive description of the full range of each species' echolocation calls. The notion of the most common type of call recorded for each species is derived from experience obtained conducting bat surveys and comparison with voucher calls recorded prior to the collection of specimens at initial development of the Anabat system. The structure of these calls may represent ordinary situations that bats are encountering (and thus be more likely to be recorded). Distinct variations of these structures may be the bats' response to different surroundings or environmental factors.

Comparing unknown calls to common calls for each species may be a dangerous tactic. Documenting these common calls is, in the long run, one way of contributing to typifying the echolocation behaviour of any species. At the very least, different common calls of the same species need to be documented across biogeographical regions.

The usefulness of the shapes system proposed in this paper is apparent when bat workers try to communicate their experience and find it difficult because of lack of terminology. For example, Thomas et al. (1987) stated that upper frequencies are generally weaker in intensity than lower frequencies, and may become attenuated with distance. This does not provide a reliable parameter for use in species recognition. Therefore, Characteristic and Final frequencies, being more intense and thus less distance sensitive, have advantages for acoustic identification provided they are referred to distinctly. Most workers would refer to Characteristic frequency as the end frequency of any pulse or its 'tail', but as demonstrated here, this depends on the shape of the pulse in question, thus a distinction must be employed.

The concepts and terms presented in this paper are an initial attempt to develop a consistent acoustic language among bat workers, that is intended to facilitate the much needed exchange of information.

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